

SOME ASPECTS OF THE BIOLOGY AND BEHAVIOUR OF *PARALUCIA PYRODISCUS LUCIDA* CROSBY (LEPIDOPTERA LYCAENIDAE) AT ELTHAM, VICTORIA

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Field observations of the Eltham Copper butterfly demonstrate that anecdotal history has a basis in the biology of the species. Its preference for small food plants results from a strategy to optimise nocturnal travel distance consistent with providing sufficient biomass to complete development. Cases of overgrazing may cause larvae to cease feeding until regrowth occurs, thus delaying pupation and producing a bimodal adult emergence. The northwesterly aspect of the colonies is a consequence of the basking habit of the adult males and the vertical spiral flights are territorial encounters. Further study is required to elucidate the tripartite ecology of butterfly-food plant-attendant ant, to establish oviposition cues and the relationship between the ant breeding colony and its satellites where butterfly larvae are tended. The contributing factors to the low vagility of the species are yet to be determined but they possibly include patch dynamics of a restricted ecosystem and the as yet unknown mechanism for mate recognition. Colony management practices must recognise that delayed pupation due to overgrazing by some individuals means that there is no period when food-plants can be guaranteed to hold no life stages of this species.

PRIOR to a public campaign to preserve some areas of its remaining habitat at Eltham, little information had been published about the Eltham Copper butterfly, a subspecies of the Dull Copper *Paralucia pyrodiscus* (Rosenstock).

In his description of the subspecies, Crosby (1951) noted that the larvae fed on *Bursaria spinosa* (Pittosporaceae) with almost always a few small ants in attendance. At Eltham the adults emerged early in December and were most abundant about Christmas time with only occasional specimens remaining by early February. Common and Waterhouse (1972) identified the ant which attends the nominate species as *Notoncus* sp., recorded that the larvae feed at night, and noted that the life history and feeding habits of the subspecies are similar to those of typical *pyrodiscus*.

Appended to a deputation to the Minister for Conservation, Forests and Lands seeking preservation of the butterfly's Eltham habitat was a review of current knowledge (Crosby et al. 1987) which included:

the larvae have a distinct preference for plants of small stature, up to 0.5 m height;
it is possible that the subspecies is bivoltine;
adults are generally active on sunny days during late morning and early afternoon;
the habitat of all known Eltham populations is box-stringybark open forest on dry northwest aspects.

New (1987) commented that the larvae largely feed on plants which are stunted and apparently unhealthy.

A small, breeding colony had been known to the author for over ten years at a site in the West Riding of the Shire of Eltham, Victoria. In December each year adults were seen flying but few specific observations were recorded. Because of these regular sightings it was not realised that the species was considered to be endangered until that was reported in the local press (Calafuri 1987). Detailed observations of larvae and adults were then made between 28 March 1987 and 25 March 1988 and they provide the basis for this report.

STUDY AREA AND METHODS

The Eltham Copper Butterfly Draft Management Plan (Vaughan 1987) listed all known sites in a confidential supplementary appendix so as not to reveal their locations to unscrupulous collectors. Site E is the one where this study was done. It covers an area of 25 × 10 m and supports a fairly natural remnant of the local association of Longleaf Box (*Eucalyptus goniocalyx*), Yellow Box (*E. melliodora*) and the introduced Cootamundra Wattle (*Acacia baileyana*), with an understorey of Sweet Bursaria (*Bursaria spinosa* var. *spinosa*), Gold-dust Wattle (*A. acinacea*), Drooping Cas-

sinia (*Cassinia arcuata*) and Small-leaf Clematis (*Clematis microphylla*).

Because of the reported endangered status of the species no specimens were collected or handled; no search for pupae or investigation of the ant nests was made; no translocation of larvae or marking of adults was attempted, even though these actions would have yielded additional valuable data. Only visual observations, times and air temperatures were recorded. Larvae were observed by torchlight but, as this often caused the larvae and their attendant ants to retreat, only a few bushes were sampled each evening to cause minimal disruption to feeding patterns.

Specimens of the ant were forwarded to the National Museum of Victoria and identified as *Notoncus enormis* (K. Walker, pers. comm.).

OBSERVATIONS

Larvae

Twenty-nine bushes, ranging in size from 340 mm to 2000 mm were host to larvae. Table 1 shows the height of each plant and the maximum number of larvae seen on it during the period. Those entries marked with an asterisk designate bushes where larvae were seen to be present but not counted; they have been attributed with only one larva so the total of 84 is probably an underestimate of the colony size.

During the period 28 March 1987 to 17 January 1988, 331 observations of larvae were made, and on 411 occasions no larvae were seen. Larval absence was due to inclement weather, complete defoliation of the host plant, the presumed start of pupation, or mortality.

Temperature. Air temperatures on evenings when searches were made ranged from 7.5°C to 28.5°C but larvae were never seen to emerge at temperatures less than 10°C. Ground temperatures adjacent to the ant and larvae refuge nests were about 1°C lower than air temperature. Rain also inhibited larval feeding.

Plant size. Generally the *B. spinosa* bushes were upright, single-stemmed and bushy; a few were multi-stemmed and lax, and some of the taller plants were bowed over to the extent that the upper part of the stem was parallel to the ground. The figures for height given in Table 1 are the length of the plant rather than the distance of its tip above ground level. This measure was used to give a better indication of the length of travel for a larva to reach the youngest foliage. *B. spinosa* hosts are log-normally distributed (Fig. 1) with

60% of the plants being less than 1 m in length and only 10% exceeding 1.5 m.

Overgrazing. When the number of larvae per plant was high, or the size of the plant was small, overgrazing occurred. In some instances bushes were totally defoliated and larvae, with attendant ants, were found wandering on bare branches. Regeneration would generally start to occur within a few weeks although some plants did not recover. Larvae did not persist with their nocturnal visits for long after the foliage had been completely grazed. It would seem that those which survived remained within the ants' nest until new leaves were available.

Bushes #G and #BB were contiguous and some of their branches were touching. On one occasion, prolonged exposure to bright torchlight caused a late instar larva on #BB to retreat down the trunk to a nest at its base. The two plants hosted

Bush	Height (mm)	Max. no. larvae
A	770	6
B	630	3
C	1650	6
D	1130	4
E	2000	1*
F	850	15
G	500	4
H	420	4
I	710	4
J	500	6
K	430	1
L	590	1
M	720	1
N	1230	1
O	950	1*
P	420	1
Q	1660	1
R	1140	4
S	760	1
T	1110	1*
U	850	2
V	1220	1*
W	1010	1*
X	1070	1*
Y	340	4
Z	530	3
AA	540	1
BB	600	3
CC	1360	2
Total		84

* Larvae present but not counted; attributed with '1' to give conservative colony total.

Table 1. Host plant height and larval numbers.

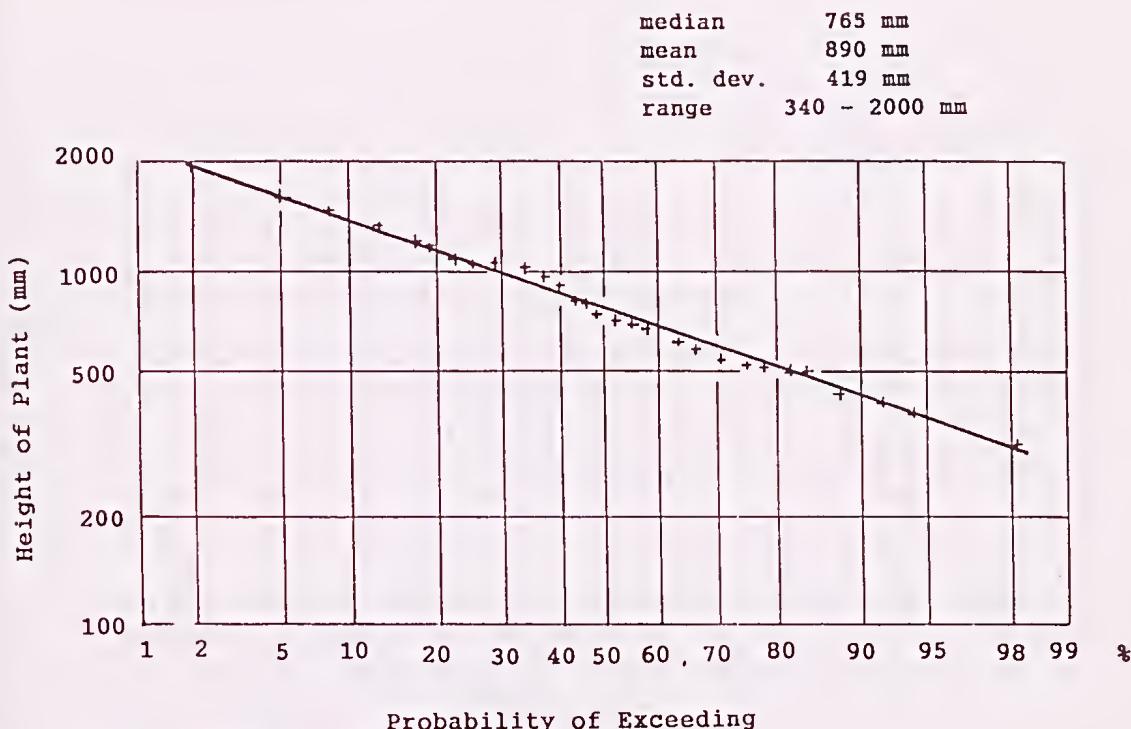


Fig. 1. Log-probability plot of host plant height.

separate populations but #BB had been defoliated while #G remained leafy throughout. This case seems to suggest that the larvae stay loyal to their own bush and ant nest, even though alternative food may be readily available.

It would seem possible that defoliation of the host plant and the consequent enforced starvation of the larva could result in a delayed pupation. As a crude measure of the food available to each larva, the height of each bush was divided by the maximum number of larvae that it had supported. This number was plotted against the latest date on which caterpillars were seen on the bush, with the assumption that this represented the onset of pupation (Fig. 2). Whilst the points are broadly scattered there is a general trend towards a later pupation when there is a lower available food resource.

Instars. Four instars were regularly seen and recognised by eye according to size: 5–8 mm, 10–12 mm, 15–17 mm, and 19–22 mm, and the smallest has darker anal and thoracic plates.

These probably correspond to the third and subsequent instars recognised by Braby (1990). Larvae which were first or second instar (ca. 3 mm) were found on 9 April, 25 April and 17 May; they were probably the progeny of late-flying adults.

Adults

Flight periods. The earliest adult to be seen in the colony was a male on 19 December 1987 at 1155 hours (Eastern Summer Time) when the temperature was 18°C. There seemed to be four flight periods during the season with the peak of activity occurring from the 6–9 January (Fig. 3).

Temperature. Sunlight and an adequate temperature seem to be a prerequisite for adults to become active in the colony. Fig. 4 shows that there is a tendency for earliest flight time to occur later in the day if air temperatures are lower ($r = -0.33$, $n = 21$). On a typical day activity commences about 1030 hours and is virtually over by 1600 hours. Late in the day when the site is in

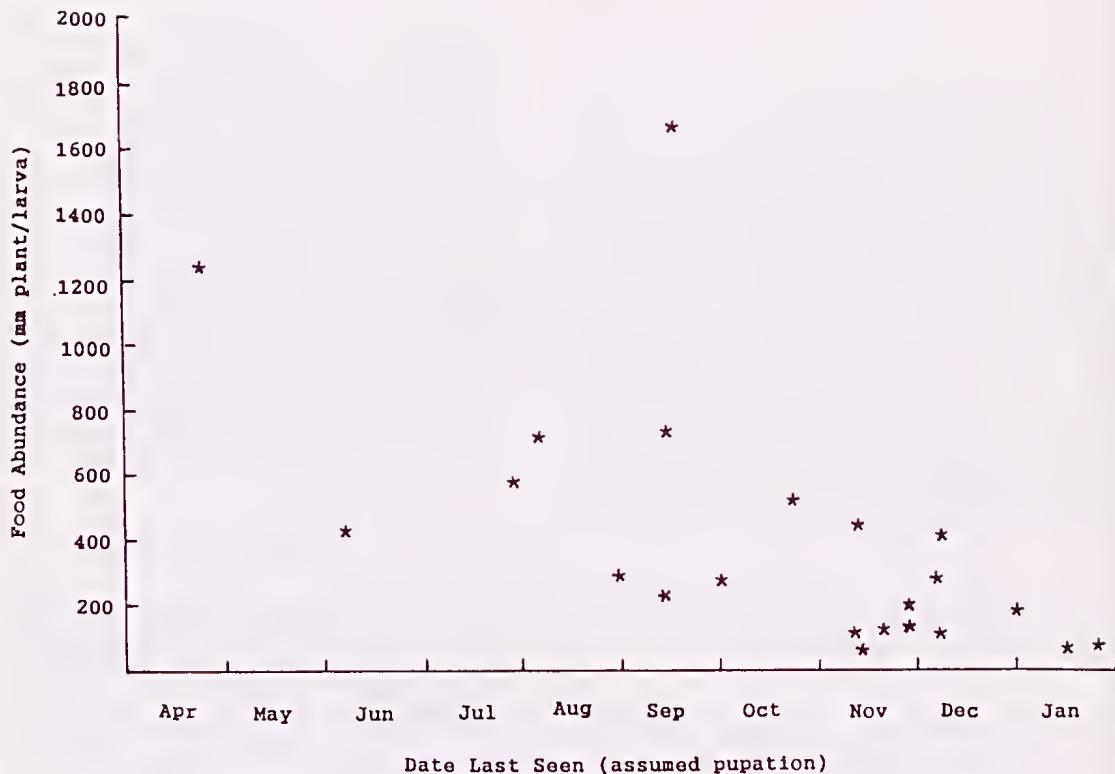


Fig. 2. Relationship of pupation date with food resource.

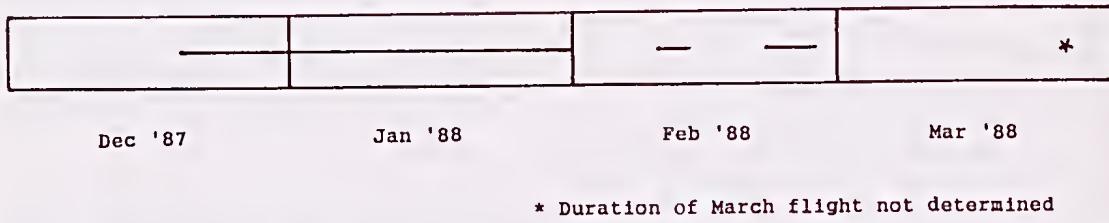


Fig. 3. Flight periods for adult *Paralucia pyrodiscus lucida*.

dappled shade the adults move to taller *Bursaria* plants on the edge of the colony where they are in full sunlight.

Flight patterns. The most obvious activities in the colony on a warm sunny day are adults either basking in the sunlight or performing a spectacular eireling flight. Four different flight patterns were

observed involving males: (a) slow fluttering; (b) 'exploratory'; (c) eonspecific spiral; and (d) other spiral. More detailed descriptions are given in the Appendix.

Neither of the behaviours that consisted of a spiral flight with another insect included female *P. p. lucida*. Every instance appeared to be a male defending a territory against a eonspecific or

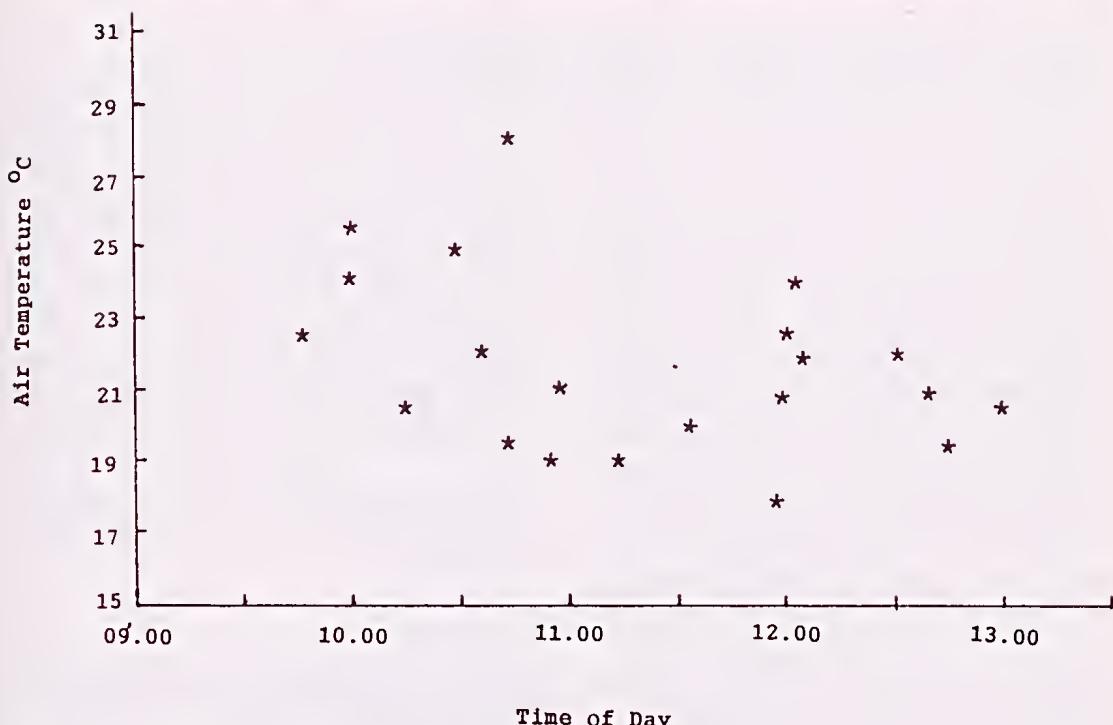


Fig. 4. Air temperature and start of flight activity.

another species that appeared to give the same stimulus or pose a threat. Female flight was similar to the male type (a) but usually closer to the ground.

Fifty-six flights of type (b), (c) or (d) were timed and the results are summarised in Table 2. Sometimes returning males were retriggered before perching, but on each occasion the additional flight time was very short and the total was within the range of the other observations. Exploratory flights of type (b) on average were shorter than those which involved a territorial element. The time spent away from the perch is significantly lower for type (b) exploratory flights than it is when the male is triggered by a conspecific (one-tailed t test, $P < 0.05$) or with the pooled results for all butterfly triggers ($P < 0.05$). Although it is not statistically significant, the average time spent 'investigating' another species is shorter than that required for a territorial defence. Territorial flights occurred more often than the other flight types.

Basking. When conditions were still and sunny, male and female adults basked with their backs facing the sun and wings opened. It was common

	No apparent trigger	Triggered by <i>P. p. lucida</i>	Triggered by other butterfly spp.
Number	13	28	15
Mean (sec.)	20.5	31.0	27.5
Std dev.	13.7	19.5	25.0
Range (sec.)	3-50	6-69	2-87

Table 2. Duration of exploratory or triggered flight by males.

to see a butterfly land, rotate its body so that the sun shone on it from behind, and then spread its wings to a dihedral angle of 120° . During a long basking period position was adjusted to track the movement of the sun. Wind, even a light breeze, was sufficient to cause basking butterflies to close their wings and show only the cryptically coloured undersides. Clouds passing across the face of the sun would also cause the butterflies to close their wings. However after a few minutes they would open them to about 30° dihedral angle and then a little later to 90° , returning to the open position

when the sun reappeared. The change in brightness seemed to cause the initial closing, not the absence of direct sunlight. On warm, but clouded days adults could sometimes be found basking with a full 120° wing opening oriented so that their dorsal surfaces would be normal to the direction from which the sun's rays would have come if there had been no cloud cover. The most common basking position was head up but adults perched on pendant branch tips sometimes assumed a head down position but still with their dorsal surface normal to the sun's direction. Occasionally a basking adult would rotate through ninety degrees and adjust its wing angle so that the sun would strike one wing normal to its surface.

Males and females, when in the 'wings closed' position, sometimes performed a display in which they slowly moved their wings alternatively in a scissors-like motion parallel to their body.

Mating. Newly emerged female *P. p. lucida* were first seen on 30 December 1987, eleven days after the first of the males had emerged. Only one attempted and one successful mating was observed. A female entered the colony and triggered a male to flight. They performed a close fluttering flight along the ground for a metre or so, and then landed with the male 20–30 mm behind the female, both facing in the same direction. The male started to quiver its partially opened wings very rapidly, perhaps to activate scent scales from what could be a black sex brand at the distal end of the cell on its forewings. (The female lacks that marking.) After a few seconds of wing quivering the female flew with the male following but the male appeared to give up the chase after a few metres and returned to its original perch.

On a later occasion a small male mated tail to tail with a large female for four minutes and then took up a perch from which it spiralled with other overflying males. Nine minutes after the first mating had finished a second female arrived. The male landed just behind and fluttered its wings rapidly. It then moved into the tail to tail position and mated for 2 hours 18 minutes.

Egg laying. On 3 January 1988 a female was seen to lay two eggs on a food plant that was about 1200 mm high. No *Notoncus enormis* were present, nor did they appear later in the day or that night. On only one occasion were *Notoncus* ants found foraging in broad daylight, and that was on an early October morning. They usually emerged about half an hour before sunset. No sightings of the ants were ever made on plants that were not hosts to *P. p. lucida* larvae.

Of importance was the discovery of three eggs on the underside of a leaf on a small potted *Bursaria*, one of two that had been placed in the colony. This plant had never been seen to have *Notoncus* on it and there was no sign of a nest at its base. Five days later, in the early morning, one of the eggs was found to have disappeared; by late in the day they had all gone. No predator was found, but on another plant a lacewing larva of the genus *Chrysopa* seemed to be attempting to eat an egg. In the first week of February 1988 one of the potted plants had 3 hatched eggs on it and the other plant had 2 hatched and one unhatched eggs. These plants never did become larval hosts but adult females were obviously prepared to lay without the stimulus of an attendant ant.

Vagility. Occasional observations of butterflies away from the core of the colony are detailed in the Appendix.

Second generation

Sixty-four eggs were found on 13 plants, in 35 separate clusters (Table 3). Most of the eggs had been laid underneath leaves, but occasionally they were found on the trunk or a branch, on top of the leaf, or in the leaf axil. The first egg was found on 3 January; by 21 February, forty-one of the sixty-four had hatched, a 64% success rate.

The batch of six eggs was located on 15 January 1988 and one week later they had all hatched. Two larvae approximately 2 mm long were seen on the trunk and side branches about 0.3 m above the ground attended by palpating *N. enormis*. By 17 March there were four larvae about 10 mm long feeding on the plant, probably fourth instar.

Later in the season larvae were found on 16 plants: 10 used in the previous season and 6 new ones. One of the previous season's plants where eggs had been located had no larvae, and four of

Cluster size	Number	Total eggs
6	1	6
4	1	4
3	5	15
2	11	22
1	17	17
Total	35	64

Table 3. Egg cluster size for second generation (64 eggs were found in 35 clusters).

	Number of plants in second generation which were larval hosts: in previous season	new for second season	Total
Egg batches located of which hatching successful	5	8	13
Larvae present but eggs had not been located	4	2	6
	6	4	10

Table 4. Location and hatching success of second generation egg batches.

the new season's plants that had eggs did not now reveal larvae. This is summarised in Table 4. The sample was small but it suggests that:

plants which were not hosts in the previous season tended to have a lower success rate than those which had been hosts;

in spite of the previous point, a substantial part of the colony can form on plants that were not previously hosts.

Other taxa

Observations of other invertebrates which have the potential to compete for the resources required by *P. p. lucida* or to become a predator are given in the Appendix.

DISCUSSION

Stunted plants and delayed pupation

Most authors who have discussed the larval biology of *P. p. lucida* have commented on the stunted form of its host plant (Braby 1990; Crosby 1987; Crosby et al. 1987; New 1987). Of the 29 bushes in the West Riding colony that contained larvae, 60% were less than one metre in height (Fig. 1). Because the larvae must travel from the ant nest at the base of the plant to the leaves to feed, there must be an optimal size that minimises the energy expended in travelling but provides sufficient biomass for the larva to reach maturity. The single observation that suggests plant fidelity, even though it may be completely grazed and alternatives are available, would place even greater pressure on optimal selection.

A misallocation in selecting plant size, or the presence of a multiple egg brood, can lead to complete defoliation of the plant before larval development is complete. It appears that the caterpillars then remain quiescent in the ant nest until leaf regeneration occurs. This would enforce a delayed pupation and the data of Fig. 2, even though scattered, do suggest that pupation occurs later if there is a lower available food resource.

Cottrell (1984) quotes the example of *Maculinea arion* (Lycaenidae: Polyommatainae) larvae which are capable of starving for long periods and then of regaining size and resuming growth when food becomes available. At least in the colony under study, delayed pupation of some individuals is a more plausible explanation for the second wave of flying adults than Braby's (1990) bivoltine hypothesis. Braby's (1990) observation that adults of the second emergence are often notably smaller is consistent with a restricted food intake during the larval stage.

Myrmecophilous lycaenids suffer the nutritional nitrogen burden of meeting their own developmental requirements as well as secreting amino acids for attendant ants (Pieree 1985). Larvae of *Malacosoma americanum* (Lepidoptera: Lasiocampidae) preferred young leaves to mature ones in choice tests (Peterson 1987) and those fed on mature leaves alone showed lower pupal weight, poorer survival and less efficient growth. Cottrell (1984) noted that many lycaenids feed exclusively on plant parts that are especially rich in nitrogenous compounds such as new terminal shoots, buds and flowers. It might be a better strategy for a larva to await nitrogen rich regrowth on its original plant rather than transfer to another food plant of old growth even if it means a delayed ecdysis.

In comparing butterflies which lay eggs singly or in clusters, Stamp (1980) postulates that dispersed eggs may be advantageous for parasitoid and predator avoidance; single larvae are less likely to defoliate their host plant and have to find a new food source; or there is reduced competition for pupation sites. While she considered that it might be advantageous for female lycaenids to deposit eggs in clusters due to the larval association with ants her review of the literature found no apparent relationship between egg clustering and mutualism of caterpillars and ants. Kitahara (1981), using wider sources, asserts that there is a strong association between egg clustering and myrmecophily among Australian lycaenids but refrains from speculating on the

nature of any causal relationship. However, in his sample, 35% of species laying eggs singly have an obligate myrmecophily and *P. p. lucida* should fall within this group as it lays singly or in small clusters (Table 3; Vaughan 1988). Laying single eggs or small batches is a practice consistent with a species that should optimise its host plant size.

A secondary consequence of heavy grazing, even to the extent of complete defoliation, on optimally sized bushes is that the plants will remain stunted and thus exhibit symptoms of poor health (New 1987) or, mistakenly, other debilitating causes (Crosby 1987). It is highly likely that it is grazing which keeps the larval hosts small, not phenotypic differences (contra Braby 1990; Vaughan 1987, 1988).

Basking behaviour and territoriality

The most obvious behaviour in an Eltham Copper colony on a sunny day is basking and vertical spiral flights involving two, or rarely more, butterflies.

Almost invariably a basking butterfly will sit with wings spread and normal to the sun's direction. Basking would appear to be a mechanism primarily for thermoregulation. Generally activity commences in the colony about 1030 hours and is virtually complete by 1600 hours. A species which basks from late morning to mid afternoon will naturally tend to face northwest and this is consistent with observations of site aspect by Crosby (1987), Crosby et al. (1987) and Vaughan (1987, 1988).

Scott (1974) categorises three mate-locating behaviours for butterflies: perching, patrolling and pheromones. He did not consider defense of a perching spot to be true territoriality because the location could drift as the day progressed or with changes in lighting or weather. Vertical encounters by perching species were seen as an attempt to determine the sex of the other participant. Arnold (1983) describes the behaviour of five lycaenids which fly out from their perches to investigate passing insects and generally return if the other is not a conspecific male (*Callophrys mossii*, *Plebejus icaroides*, *Euphilotes enoptes*, *E. battoides*, *Apodemia mormo*). *C. mossii* routinely investigates other males that enter its territory and the ensuing encounters are characterised by vertical flights. Certain perching sites are obviously preferred. In an experimental field study of *Pararge aegeria* (Lepidoptera: Satyridae) Davies (1978) determined that males competed for sunspots which gave sufficient warmth to enable them to remain active and they were the

best sites for locating females. Spiral flights were a territorial defense and the resident always won, irrespective of age or condition. They were not, as proposed by Scott (1974), a means to determine the sex of the other participant.

With *P. p. lucida* three flight types from a perch were observed: triggered by a conspecific male; triggered by another butterfly species; and flights with no obvious trigger, termed here 'exploratory'. Table 2 shows that exploratory flights were significantly shorter but there was no statistical difference between the two triggered flight types. No spiral flights from the colony under study involved a female (contra Vaughn 1988) so the behaviour noted is consistent with the defense of a perching site as in Davies' (1978) experiments. Distinctively marked or damaged resident male Eltham Coppers were seen to win contests and preferred perching sites did migrate with the movement of the sun.

Mate location

Other than Vaughan's (1988) misinterpretation of the male territorial flight as a courtship dance there is no published description of mate location and copulation for this species. Edwards & Common (1978) mention the flight of the congeneric *P. spinifera* as being close to ground near the foodplant and slower than the male. This is an apt description also for the flight of females at this site. However there are occasions when males make low, slow fluttering flights which cannot be distinguished by the human eye from the style of female flights. A male which sights the female from a perch and then approaches her must be responding to some visual or olfactory clue. Wing pattern dimorphism is slight and the different shape of female wings is possibly not distinguishable in flight. Obara (1970) demonstrated that the wings of *Pieris rapae* females reflected near ultraviolet radiation while those of males did not. Males detected females and models by this difference. It is feasible that *P. p. lucida* also uses a sex differentiation of this type and is worthy of an ultraviolet sensitive photographic study.

The wing quivering action of the male prior to mating is consistent with the release of pheromones from androconia. Scoble (1992) suggests that pheromones usually tend to inhibit female flight rather than stimulating them to mate. Some of the lycaenids studied by Arnold (1983) exhibit behaviour that could be interpreted in this way. Androconial scales are used by Eliot (1973) as one of the character states in his phylogenetic study

of the Lycaenidae. He places *Paralucia* in the tribe Lucini of the subfamily Theclinae and this group has 'primitive' androconia which barely differ from ordinary scales. Scales from the small black wing spot of male specimens are linear with multifid distal endings and do not appear to differ from other black wing scales. Female specimens in the collection of the Museum of Victoria do not have a corresponding black spot on the forewing (K. Walker, pers. comm.) so there appears to be some sexual dimorphism. Eliot (1973) includes diagrams of scent scales from the Lycaenidae which are entire and not plumose as in the typical belief about androconia, and so the scales from the previously unrecorded putative sex brand of *P. p. lucida* should not be dismissed as normal without further detailed investigation.

Host selection

The obligate relationship of the Eltham Copper butterfly with its foodplant (*B. spinosa*) and its attendant ant (*N. emarginata*) raises a number of questions about host plant selection by the ovipositing female. Choosing the optimal size of foodplant is a related decision.

Sweet Bursaria must have some special property that causes the Eltham Copper to use it exclusively as a larval host. Because of the additional nutritional load necessary to produce ant attracting secretions, Pierce (1985) expects selection to favour ant-tended lycaenids which specialise on protein rich plants. It would be an informative study to see if *B. spinosa* exhibits any nitrogen enhancing adaptations such as those summarised by Bowen (1981): nodules; proteoid roots; cyanophyte or other mycorrhizal symbionts.

Brown (1955) described the ant species as being a nocturnal or crepuscular above-ground feeder and the observations of both Vaughan (1988) and myself (pers. obs.) support this for the local colonies. The presence of ants in daytime is not a cue for the female butterfly.

Other butterfly species have solved the mutualism problem by ovipositing in the presence of the appropriate ant or by another taxon (particularly Hemiptera) which also attracts the particular ant species (Atsatt 1981) but this does not seem to be the method employed by the Eltham Copper. Egg laying on potted plants that had never contained an ant nest supports the belief that ants or other taxa do not determine the oviposition site. According to Cottrell (1984) many tribes in the Theclinae oviposit directly onto plant surfaces utilising only cues that derive from the plant itself.

Vaughan (1988) noted that ant nests located beneath Sweet Bursaria at Eltham had few workers and no apparent brood but there was a major ant colony within the vicinity. He quotes similar observations by Keith Hately at Kiata.

The most parsimonious hypothesis is: adult females are able to detect the host plant and lay small egg clusters on appropriately sized bushes; nocturnal foraging ants locate eggs at random and then establish a temporary nest at the base of the plant to await larval hatching. This assumes that ants can identify *Paralucia* eggs through olfactory means but it does not address the relationship between the temporary nests and the main colony. There is no selective advantage in maintaining small cadres of worker ants remote from the breeding colony, so there must be some connection between the secretion collection sites and the main colony. Perhaps some main colony workers travel each night to the temporary nests to collect and transport lycaenid fluids by trophallaxis. Further observations and manipulative experiments to test these suppositions would be invaluable.

Vagility

Within 100 metres of the study site is a remnant Bursaria/Long Leaf Box Association that has been preserved within the housing development. It appears to be typical Eltham Copper habitat and possibly represents the vegetation that covered much of the land that had been cleared in the few years prior to this study. Despite numerous visits to the site during the season, no larvae or adults were found. This was neither source nor sink for adults of the local colony.

The greatest distance that adults were found from the centre of the colony was 40 metres and even this distance was a rare occurrence. If this is, indeed, a true measure of their vagility, the colony has possibly been isolated for at least twenty years with no apparent deterioration in its viability.

In his study of endangered American lycaenids Arnold (1983) noted that the strong correlation between the occurrence of adults and the presence of larval foodplants and nectar resources indicated the stringent microhabitat needs of each species. Also, mate location by rare species is optimised when the adults are aggregated whereas for common species there is no selective advantage in being clumped. These habitat and behavioural requirements appear to have selected for individuals with low vagility. The same conclusion can be reached for the local populations of the Eltham Copper.

CONCLUSIONS

Much of the anecdotal history of the Eltham Copper Butterfly can be explained in terms of the biology of the species. Its preference for small food plants probably results from a strategy which optimises the energy required for nightly travel distance and adequate biomass to complete development. The stunted or diseased appearance of the bushes is generally due to overgrazing.

A second flight peak in each season is more likely to be due to delayed pupation of individuals which have been restricted to an under-sized food-plant rather than to a second rapidly developing generation.

Basking in late morning to mid afternoon is facilitated by localities with a northwesterly aspect and territorial defence of preferred sunny patches as basking sites leads to spectacular spiral flights between males.

Further studies on mate recognition, oviposition cues, and the tripartite ecology of butterfly-plant-ant would be of great value.

Because of the delayed pupation of some larvae within the colony, due to overgrazing, they can still be present when the next generation of eggs is laid by early emerging adults. The management implication of at least one stage always being present on *Bursaria* plants is that suggestions of slashing to keep the stature of bushes low and therefore attractive to the butterfly (Vaughan 1988) will result in the loss of some individuals, either as egg or larva.

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- (d) a basking male will be triggered by a species other than another *P. p. lucida* male. On most occasions the stimulus was the Common Brown butterfly (*Heteronympha merope merope*) but *Geitoneura acantha ocrea*, *Ocybadistes walkeri sothis*, and *Zizina otis labradus* also triggered the spiral flight. A wasp of unknown species, and a syrphid fly, did not evoke flight when they flew over a basking male at a distance that would be expected to cause a reaction if another butterfly had been involved.

Vagility

Almost all of the adult activity was confined to the area of the colony where larvae had been observed, or to a sunny site thickly covered with *Bursaria* bushes 1 to 2 m tall, about 5 m to the south. On five occasions adults were found further away:

- a sleeping male roosting about 6 m northwest of the centre of the colony;
- males performing a spiral dance 17 m northwest;
- a male basking 23 m northwest;
- females, on two occasions, basking about 40 m north of the colony.

APPENDIX

Additional or more detailed observations than those presented in the main text:

Male flight patterns

Four flight patterns were recognised:

- (a) a slow fluttering flight across the tops of the larval food plants and through the undergrowth, usually restricted to 0.5 to 2 m above the ground.
- (b) a basking male will fly rapidly from his perch and return to the same spot within 20 seconds.
- (c) a basking male will be triggered to flight by an overflying male. They spiral about each other rapidly and often rise to heights up to 10 m. Usually within 30 seconds one of the males will return to the original perch. On a number of occasions the male that had been triggered was sufficiently distinctive to be recognised as the one that resumed the perch site. This has all of the hallmarks of a territorial encounter. It was not unusual to see a third male join a spiralling pair.

Other taxa

Between late August and late September *N. cornuta* were observed tending aphids on bushes which also hosted the butterfly larvae. In one instance two larvae were surrounded by aphids identified as *Macrosiphoni euphorbiae* (Thomas) (G. Berg, pers. comm.). This is the Potato Aphid, a polyphagous species, probably present by coincidence.

During October a number of *B. spinosa* plants in the colony and in other local plots displayed a strong fasciation of the terminal leaves. In October 1995, Dr Laurence Mound (Natural History Museum, London) examined specimens of thrips from the colony's *Bursaria* galls and found them to be *Neocecidothrips bursariae*.

Another minor and indirect food competitor was a psyllid from the subfamily Spondylaspinae. They were discovered as spent husks adorning the backs of their predator, a lacewing larva (*Chrysopa* sp.). They pose no threat to the butterfly colony.

It is often surmised that the *P. p. lucida* larvae attract the ants with secretions from their dorsal and dorsolateral organs in return for protection from predators and parasites (Hinton

1949; Malicky 1970). On one occasion two ants were seen to shepherd a 3 mm larva along the trunk and beneath the arched leg of an *Olios*

diana. The spider flinched its leg as the ants passed as though it had been bitten; it then sidled a short way around the trunk.